

AMAZONIANA	IV	t	103 – 133	Kiel, März 1973
------------	----	---	-----------	-----------------

(From: Cooperation between Max-Planck-Institut für Limnologie, Abt. Tropenökologie, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus-Amazonas, Brazil)

## Crocodiles and the nutrient metabolism of Amazonian Waters

by

Ernst Josef Fittkau

In a previous study (FITTKAU 1970), the possible significance of caimans for the bioeconomics of nutrient-poor, Central Amazonian waters was outlined. Impetus for the development of this hypothesis came from field observations which suggested that an ecological correlation existed between the sizes of the crocodile population and the fish crop. Caimans were almost totally eliminated from Central Amazonian waters, especially between 1940 and 1950, and fishermen hoped that larger fish crops would result. However, in spite of the absence of changes in other conditions, fish crops noticeably decreased.

One may have reservations about the reliability of such reports. Yet it is a fact that the former structure of the ecosystem in these waters, undisturbed except for the removal of a single, if important, part of the biomass, has been destroyed. A new and different ecological balance must have been established. It remains uncertain for the time being whether it was possible for the former fish production to be maintained in the new system.

### The Structure of Central Amazonian Ecosystems

The same ecological principles which govern the terrestrial ecosystem of the Central Amazonian region, the rain forest, determine the character of the freshwater systems, although they are expressed in a different manner. This may be seen in the extreme limnological conditions which arise from the hydrographic, geochemical and biological features of electrolyte-poor Amazonian waters. Before we take up the special problem of the caimans, the general principles of ecological interrelationships in Central Amazonia as we see them should be set forth to form a basis for the presentation.

The extensive Central Amazonian lowlands, which are not submerged during the annual high water levels, are called 'terra firme'. Geochemical reserves in these areas, when they exist at all, are in forms which make them unavailable to the materials cycles of the forest. The soils which have formed on the blankets of tertiary lacustrine and riparian sediments



here are thoroughly weathered and leached. Practically all of the essential nutrients are bound within the living and dead biomass.

Of the total living and dead biomass, by far the largest part is represented by plant materials; the fauna makes up only a small fraction. Quantitative investigations of the vegetation and ground fauna, supplemented with calculations and estimations of the remaining fauna, yielded the following values for fresh biomass: about 1000 metric tons of plants and about 0.2 tons of animals per hectare (FITTKAU & KLINGE 1973).

Such a high ratio was previously unknown, and not expected, in a tropical rain forest. Yet in view of the fact that the food chain in this forest is based primarily on non-living products and dead tissue of primary producers, it may be understood as a direct adaptation to the harsh geochemical conditions, which appear to be common within a tropical forest biome. One can also understand the extraordinarily rich diversification of plants and animals of the rain forest biocenoses, into a large number of different species within a few basic Lebensformen (life-forms), as an adaptation to this lack of nutrients: without this rich diversity and rapid turnover of materials, the nutrient cycles could not be completed with such small losses under wet-tropical conditions. As an illustration, about 18.4 kg of calcium are dropped to a hectare of forest floor as litter annually in the area of these investigations (KLINGE & RODRIGUEZ 1968); yet in spite of the heavy rainfall, Ca cannot be measured in the streams of the region by any methods tried so far (FITTKAU 1964). Of course, a small quantity of nutrients is still lost continuously from the ecosystem in surface runoff and ground water, but only in amounts that can be replaced by rain water (ANONYMOUS 1972).

We believe then, that there is an ecological principle here which governs the formation of this rain forest ecosystem and guarantees its survival; the system maintains losses of nutrients from the cycles at a minimum, and continually assimilates as many additional, allochthonous nutrients as possible.

By this principle, it is a biological necessity in this kind of environment that there exist a large, richly diversified plant biomass and relatively shortened nutrient cycles, which are completed largely in the absence of higher animals. The large biomass of living and dead plants insures a large reserve of nutrients, especially in comparison to the substratum with its essentially negligible reserves. The highly differentiated biota, rich in both individuals and species (KLINGE counted 505 species of higher plants on 0.2 ha – see FITTKAU & KLINGE 1973), guarantees rapid uptake of all nutrients set free by remineralization and rapid fixation of all allochthonous nutrients supplied to it. In other words, the best utilization of a small total supply of nutrients is achieved.

The geochemical poverty of this region is expressed in the aquatic biocenoses of the Central Amazonian 'terra firme' as it is in the terrestrial ones. The lack of nutrients has a particularly severe effect in aquatic habitats, because only flowing waters, in the broadest sense of the term, occur here. This is true because they are flow-through ecological systems rather than circulatory ones, as those in forests and lakes are. The concentration of essential electrolytes are usually so low in these running waters that scarcely any primary production can take place. Phytoplankton and Aufwuchs are present in extremely small quan-

ties, and submerged macrophytes are very rare. The food chains, whether in stream, river or river-mouth lake, are constructed mainly on a foundation of allochthonous organic material originating in other ecosystems. In streams and rivers, it comes from the forest. The lower reaches of the rivers also receive materials from the main rivers, including the Amazon and its tributaries, which are richer in nutrients. One of the forms in which this material enters is the biomass of immigrating fishes and other vertebrates. The principle governing the forest ecology is obviously applicable to these limnetic biocenoses, as well: presence of a richly diversified and relatively large biomass, rapid nutrient cycles, best possible utilization of allochthonous materials entering the system.

In contrast to the rain forest, the macroscopic, living biomass in the aquatic systems consists almost exclusively of animals. Here as in the forest, dead plant materials, especially leaves, form the base of the food chain. They serve indirectly, however, for the animals are actually feeding upon the microorganisms, i.e., bacteria and fungi, which decompose the leaves. In addition to these materials, other sources of directly usable organic matter also seem to be very important for the existence of the stream biocenoses. It appears that a qualitatively and quantitatively rich biocenosis can only be established where the deposition of such nutrient-rich organic materials as flowers, fruits, etc. and insects and other animals is particularly great (relative to the surface area and quantity of water). Fish constitute a major element in the autochthonous biomass. They also are an important biological filter for retention of the just mentioned nutrient-rich, allochthonous organic materials. The remark of KNOEPPPEL (1970), that it was almost impossible to find selective feeders among the wealth of fish species in one of the streams of the deep forest, illustrates the ecological function of these animals in the biocenosis. On the other hand, we have observed extreme feeding specialization in various insect larvae, including Ephemeroptera, Trichoptera, simuliids and chironomids. They are very skilful in trapping tiny particles in the drift (see SATTLER 1963, 1967), and are adapted to exploit the microorganisms, or fungi and bacteria, and fine detritus suspended in the water.

As the stream enlarges, the amount of allochthonous, nutrient-rich organic material per unit of water decreases. Where this occurs, a severe diminution of individuals and species in the biocenosis soon sets in.

In the broadened lower reaches of the rivers, which resemble lakes, we find a new ecological situation. As the water levels in the main river system rise and fall on an annual cycle, these lower reaches become backwater 'lakes', 10–15 m deep, filling for six months and slowly draining over the next six. The biocenosis of this lowermost section of the river has a different structure from that of the upper reaches, the forest streams, yet it is similarly diverse and especially rich in biomass. In this habitat, the wide yearly fluctuation in water levels is added to the lack of electrolytes as a strongly limiting factor. But because of the seasonally large water surface and temporary retention of the water, nutrients added in the rain should noticeably stimulate the very low phytoplanktonic production. More important still are the allochthonous nutrients entering from the nutrient-rich, productive waters of the Amazon and its floodplain, largely in the form of brooding fishes. These appear to be principally responsible for the existence of this ecosystem.



If we now attempt to comprehend the function of the ecosystem in such a 'mouth-lake' or river-lake, it is not difficult to recognize here, too, the ecological principle which governs the forest and streams of this landscape. That is, when the supply of nutrients is low, a biocenosis must have a large and richly diversified biomass. This enables the biocenosis to efficiently utilize the allochthonous input of inorganic, and in the water the more important organic, materials, and to maintain its nutrient cycles in as shortened a form as possible.

Besides the fishes, the turtles, caimans, otters and dolphins constitute especially important reservoirs of biomass in this semi-lacustrine habitat, and they are able to survive the low-water phase. They should play a double role in maintenance of the ecosystem according to the hypothesis mentioned in the first paragraph of this paper (FITTKAU 1970), as both accumulators and transformers of the essential allochthonous nutrients. Figure 1 shows the details of how the food chain is constructed and the course of materials cycles in this presently still hypothetical schema.

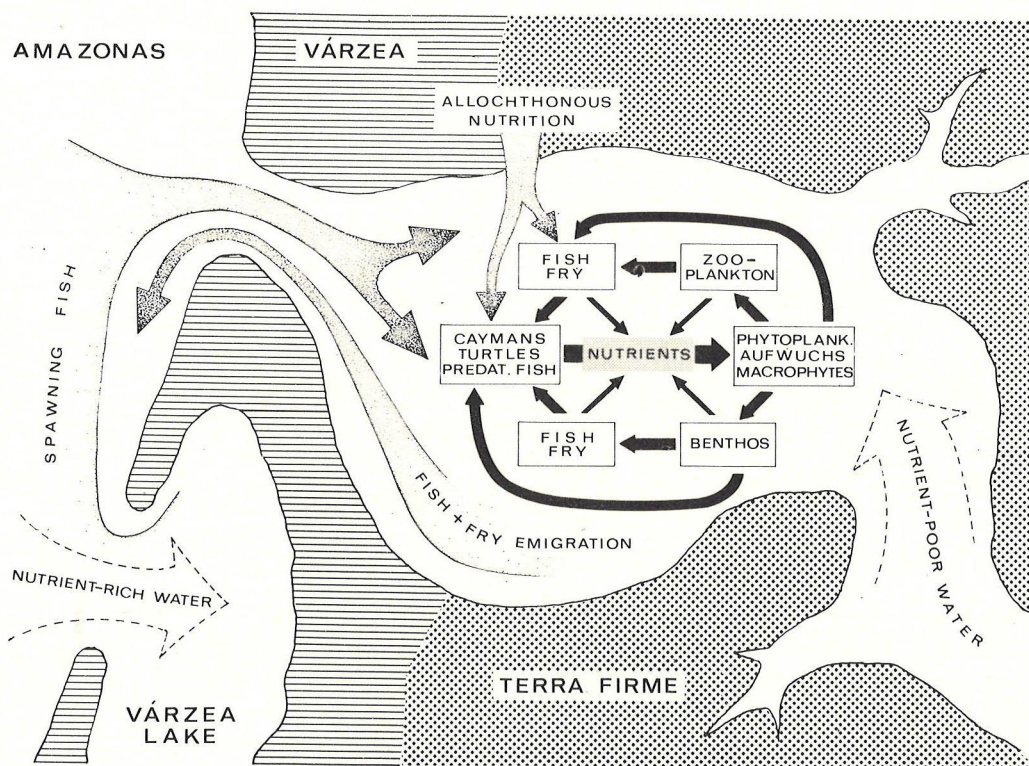


Fig. 1. Nutrient cycles in the mouth-lake of a Central Amazonian river (from FITTKAU 1976).

The large swarms of fishes which enter these electrolyte-poor waters to spawn are easy prey for the caimans and other top carnivores. The crocodiles and other piscivores excrete 'allochthonous nutrients' into the water in the form of metabolic end products, and these immediately stimulate primary production. Phytoplankton, Aufwuchs and macrophytes form the main food of zooplankton and benthos. Primary producers, zooplankton and benthos then become the basic food of fish fry and the myriads of small fishes. Fry and small fishes, finally, join the food chain to the top carnivores, closing the cycle. Part of the fry escape back into the electrolyte-rich waters of the main river system.

The goal of the present work is to reveal the amounts of nutrients released by caimans in the course of their metabolism, and the significance of these quantities of released nutrients from caimans and other top carnivores for the materials cycles of this ecosystem; i.e., whether the amounts are large enough to allow an increase in primary production. The result will show whether our hypothesis on the significance of caimans for the materials cycles of Amazonian mouth-lakes may be retained. The hypothesis represents a basic premise of the ecological principle we have presented. This principle can lead us to an understanding of the ecosystems of tropical environments which are extremely poor in nutrients and are, to a large degree, dependent on the addition of allochthonous nutrients.

While the first part of the goal we have set for ourselves, to determine the release of nutrients by caimans, can easily be achieved with sufficient precision by experimentation, the second part is beset with uncertainties and lack of precision. In order to determine whether the amounts of nutrients released are enough to influence the ecosystem, it will be necessary to conduct further investigations in the field. There are no exact data at all so far on fish migrations, nor on the biomass of fishes and their composition in Amazonian waters, either with or without caimans. The same is true for the sizes of the populations of turtles, otters and dolphins in these habitats. Even the standing crop of caimans can only be roughly estimated from older reports and a few personal observations in nearly undisturbed regions. Still, this biological component of the ecosystem which interests us is the one which may be estimated and used with the greatest certainty. One is astonished again and again at how little we presently know about the whole group of neotropical crocodiles, and this at a time when they are threatened with extinction !

## The Caimans of Amazonia

Of the four caiman species which inhabit the Amazonian region proper, two occur predominantly in semi-lacustrine waters and quieter parts of larger and smaller rivers, *Melanosuchus niger* (SPIX) and *Caiman crocodilus* (L.), the jacaré-açu and the jacaré-tinga of the Brazilians. The other two species, *Palaeosuchus palpebrosus* (CUV.) and *P. trigonatus* (SCHNEIDER) are primarily flowing-water forms which belong to the biocenoses of the flowing parts of smaller rivers and of streams (MEDEM 1958). For present purposes we need



only be concerned with the first two species. *M. niger*, the jacaré-açú, can reach lengths of 4–4.5 (6) m, making it the largest species of the Amazonian region. The largest South American crocodiles, *Crocodylus acutus* (CUV.) and *C. intermedius* GRAVES of the Orinoco basin, are usually even larger, but do not occur in Amazonia. Humboldt's oft-cited observations were of these species. *Caiman crocodilus* reaches a maximum length of 2.5 m (WERMUTH 1953), but most are mature at 1.5 m. At first, the most intensively hunted species, because of its size, was *M. niger*. Only when the demand for the hides of this caiman began to exceed the supply did the pursuit of *C. crocodilus* increase. We can get some idea of the abundance *M. niger* a few decades ago from the number of caiman hides exported: around 1950, up to 5,000,000 were removed from Brazilian Amazonia alone each year. Between 1960 and 1970, the yearly totals still were between 200 000 and 700 000, but in that decade, the numbers included the hides of *C. crocodilus* in the smaller and smallest size classes, those which had previously escaped the hunt.

The numbers that have been given are only those that have been published by government officials. The number of caimans actually killed is generally known to be far greater. It is estimated that for one officially exported skin one or two additional animals have been killed. One can say that in 1950 in the Brazilian part of Amazonian alone there were approximately 12 million of medium and large sized individuals of *C. niger* killed.

The crocodile populations must have been tremendously numerous over a century ago, for BATES (1866) wrote: 'It is scarcely exaggerating to say that the waters of the Upper Amazon in the dry season teemed with caimans as the ponds of England with tadpoles'. During a journey of five days which I once made by steamship in November, we saw almost everywhere on both sides of the way these predators, and the travellers amused themselves from morning to evening by shooting bullets through the armoured hides. They were especially abundant in the quieter bays; here they formed tangled masses which broke up with a loud commotion when the steamship went past them.' As early as 1850, WALLACE was eyewitness to intensive drives of caimans in Lower Amazonas. A quote from G. HAGMANN (1902) will provide insight into the opinions of a biologist about crocodiles at the turn of the century: 'Only recently has the slaughter of crocodiles been conducted on such a large scale, since it is done to protect the large herds of cattle from these pests.' 'I had the great good fortune during my stay in Mexiana to personally participate in the grand drama of a mass alligator hunt, where in two days, the 15th and 16th of November, about 800 animals between 1 and 4.2 m in length were rendered harmless.'

In spite of the intensive hunting of these animals in former years, one could still sight caimans regularly, mostly *C. crocodilus*, on night excursions by lamplight up the tributaries of the middle reaches of the Amazon. In the Rio Negro, about 80 km above Manaus, an *M. niger* about 4 m long showed himself to us as late as 1962. Doubtless the densest crocodile populations were sustained in the nutrient-rich waters of the Amazon and its floodplain. But their numbers were not inconsiderable in even the extremely electrolyte-poor waters of the Rio Negro drainage system. A settler on the Rio Cuieiras (a left tributary of the lower Rio Negro) gave me a reliable statement that he had caught 60 specimens of *M. niger* in a single night about 20 years ago. Today, one can no longer find the species at that site.

Only a few references to the feeding habits of caimans occur in the Literature (MEDEM 1958, 1968). In general, it is assumed that they live on fish. *M. niger* and *C. crocodilus* undoubtedly behave similarly to other species whose biology is better known, such as the North American alligator and the palaeotropical crocodiles, for example. These feed in their earlier immature stages mainly on invertebrates, then change to a preference for fishes, and as they grow older and mature, they feed increasingly on other aquatic, as well as terrestrial, vertebrates such as birds and mammals (see CORBET 1959, 1960; COTT 1963). MEDEM (1968) surely means to imply similar feeding when he says that caimans eat everything which is not a plant or a plant product. BATES (1866) reports that large specimens of *M. niger* frequently come out onto land to look for food at night. This gives us a strong indication that crocodiles also bring allochthonous nutrients into the water by this route.

Data on the amount of energy per unit time that is required by a crocodile for normal behavior and growth are rare in the literature. Furthermore, all these data refer to the North American alligator or African crocodile species. The state of our knowledge on the metabolism of alligators and caimans has recently been much advanced by the detailed study of COULSON & HERNANDEZ (1964). However, this and a series of other investigations on the physiology and biochemistry of crocodiles can provide very few useful data for our ecologically oriented line of inquiry.

#### Feeding Experiments with Caimans

We have been able to arrive at estimates of the possible abundance and biomass of caimans in a mouth-lake on the basis of data from the literature and our own experience. There is little remaining uncertainty, also, on the type of food they utilize. It remains to be determined, however, just how much food they require, what proportion of the ingested food they assimilate, and how much of it is excreted or egested. To answer these questions, we measured the amount of food ingested and the weight of two medium-sized specimens of *Caiman crocodilus* continuously for more than two years. Furthermore, during fifteen months of this time, the amounts of N, P, Ca, Mg, Na and K released by the animals were determined under both well-nourished and starved experimental conditions.

#### The Experimental Animals and Their Previous History

The two animals used in these experiments were shipped from Manaus, Amazonas, to Germany in 1967 at the age of about one month. Four other specimens of the same age and species died either during or shortly after the eight-week journey, which was made without food or water. Within two years, the two survivors grew from their initial length of about 26 cm to 90 and 100 cm. Over the same period, their weight increased from about 40 g to 2.8 and 3.6 kg respectively. Both animals were kept during this time in a concrete tank 180 x 80 x 80 cm in size, at a constant room temperature of about 28 – 30°C. The bottom of the tank, covered with stones and sand, was submerged in one half under about 15 cm of water, the other half being above the water level. The water temperature, as a rule, stayed 1 - 2°C below room temperature. A strong net was stretched over the top of



the tank to prevent the animals from jumping out. Several times a week, an infrared lamp was placed over the tank for a few hours. They were fed about twice a week on freshwater fishes, or sometimes on fresh herring, or livers and hearts from pigs and cows.

Unlike other individuals of this species which we had reared earlier in the same way, these two animals refused to eat for long periods, so that they occasionally had to be force-fed. They remained shy and did not become tamer with time; rather, they became more aggressive and dangerous, again in contrast to our previous experience. Every time they were taken from the tank to be weighed, they became so excited that they would refuse food for days or weeks thereafter. This behavior had a serious, disruptive effect on later experiments, and eventually forced us to discontinue the weighings for five months during the experimental periods.

#### Treatment of the Animals During the Experiments

Two experimental tanks, used in alternation during the experiments, were constructed of wood to the dimensions 140 x 90 x 90 cm and fitted with replaceable liners of quilted PVC sheeting. An 80 x 50 cm shelf of rigid PVC was placed just above the water line in each tank to provide a surface on which the animals could rest out of the water. These platforms were covered with large chunks of granite, which gave the animals a foothold for climbing out of the water, at the same time providing them with an opportunity to wear down their claws. The room and water temperatures were the same during the experiments as in the rearing period 28 - 30° and 27 - 29°C, respectively. The animals were regularly irradiated with infrared light. They were fed two times at first, then later up to five times each week. Both animals had to be kept in the same experimental tank during the first period of study to save space.

#### Procedure for Determination of Food Ingestion and Nutrient Release

At the beginning of each of the experiments, which lasted about 20 days, 75 l of distilled water were poured into the tank. Each day, about 2.5 to 3 l of this evaporated. If the experiments were continued longer, distilled water was added later in the experiment. During the experiments on nutrient release, the food consisted exclusively of 12-15 cm long roach, *Rutilus rutilus* (L.), purchased without selection. These fish were caught in Schulen Lake (Holstein) on 13-X-68, individually weighed, and frozen in plastic bags within 24 hours. In order to avoid contaminating the water with the food, the fish, two in each case, were hung well apart just above the water line on wire loops. Generally, the caimans took the fish so presented immediately and swallowed them whole. If the animals refused the food, the fish dried out and could be removed on the following day.

The animals were not fed for at least three days before the end of an experiment. Then they were taken from the experimental tanks and placed in rigid plastic tubes 15 cm in

diameter and 90 cm long, the head end closed by a slide valve, to be weighed. After the animals had been rinsed with distilled water, they were placed immediately in a second experimental tank filled with 75 l of distilled water.

Next, a water sample was taken out of the tank from which the animals had been removed. This was done after a thorough scrubbing of the sides and bottom of the tank and breaking up any fecal pellets which were present. When the water had been well stirred, a two-liter plastic container was filled and frozen in a freezer chest for later analysis. In the same operation, the volume of the remaining water was determined.

#### Chemical Analysis of Food and Experimental Water

Chemical investigation of frozen water samples and food for N, P, Ca, Mg, Na and K was performed in several series in the laboratory of the Max-Planck-Institut für Limnologie by methods in standard use here. The analyses were carried out by Mrs. B. Wlochinsky under the supervision of Dr. H. Klinge. Valuable technical advice on analytical procedures was given by Dr. H. Ungemach of Albaum. N and P were determined with an autolyzer by Chem. Eng. (grad.) D. Albrecht.

Great appreciation is expressed to all these coworkers, as well as to Miss E. Brekwolt and Miss Ch. Lanfer, who cared for the animals, and Miss G. Konopka, who assisted in the production of the drawings.

#### Experiments for the Determination of Food Assimilation and Growth

The courses of increase and decrease in the weights of the two animals throughout the duration of the experiments, a total of 814 days, are given by curves A and B of Fig. 2; curve C shows the mean weight for these two animals. The figure also illustrates the duration of the individual experiments and their temporal distribution over the year. As mentioned above, the feeding requirements of the animals varied widely. Their appetites dropped off increasingly in the second half of 1969. After November, animal A refused all food while animal B ate very little. This may be interpreted as a seasonal activity rhythm, for in the following year, such behavior appeared later and was not so distinctly noticeable. At that time, the animals were being forced to go for long stretches without food. The abrupt decrease in weight of animal A in February 1971 may be connected with some internal injury suffered by the animal; at the end of January, it had torn through the netting which covered the tank and fallen about 1.5 m to the stone floor of the room. After this, it refused to eat anything at all for a full month.

In order to avoid excessive disturbance of the animals, they were not weighed after experiments XIV-XVIII, but were immediately transferred into the freshly prepared tank. While the food in experiments IV-XVIII consisted exclusively of *Rutilus rutilus*, in later experiments (a-e) they were fed mainly on liver and hearts of pigs and cattle. In the experimental series a-f, the two animals were held separately to allow the determination of their individual feeding capacities.



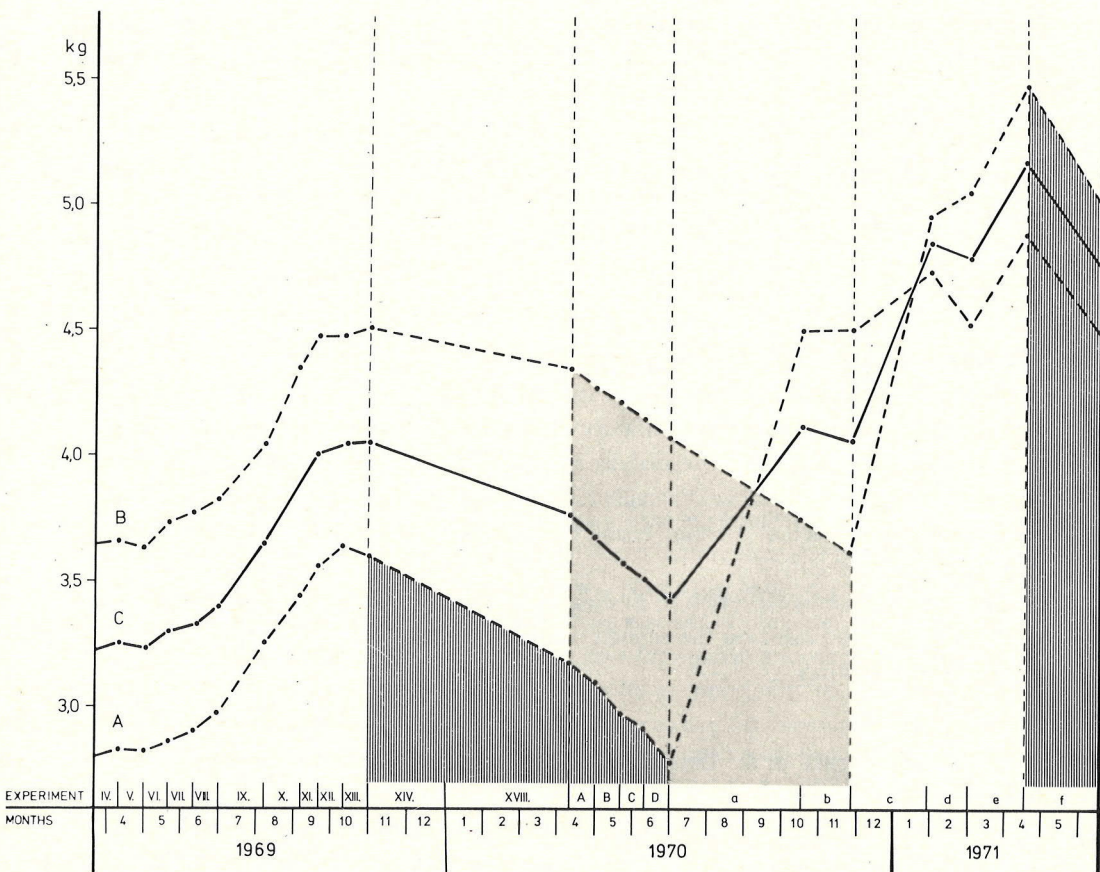


Fig. 2. Increases and decreases in the weights of experimental animals A and B. C — mean weight of the two animals. Starvation periods for animal A: experiments XIV - XVIII, A - D and f; starvation periods for animal B: experiments A - D, a, b and f; starvation experiments A - D and f.

The two phases of forced starvation covered the experiments A-D and f, and in addition, experiments a and b for animal B. Animal A had not eaten for 161 days prior to starvation experiments A-D, i.e., during experiments XIV-XVIII. Since experiments A-D lasted an additional 82 days, this animal took no food for a total of 243 days. Right up to the end of the starvation phase, its aggressive behavior remained unchanged, although in the last weeks severe emaciation and obvious weakening of the animal had set in. As soon as the experiment was completed, it fed voraciously.

Animal B, which had also refused food for a long period before the forced starvation, began to feed intensively and grow again during experiments XVI-XVIII. This is not apparent from Fig. 2, because the animals were not weighed between experiments XIV and XVIII.

It was kept without food for an additional 141 days after the 82 days of experiments A-D (i.e., during experiments a and b), a total of 227 days. In contrast to animal A, which was already malnourished at the beginning of experiment IV and did not eat well and grow again until experimental series a-e, animal B was scarcely thinner at the end of the starvation period. During the last weeks of its starvation, however, several small, festering sores appeared on its back. These healed rapidly later. The first food it was offered after the starvation period was immediately taken.

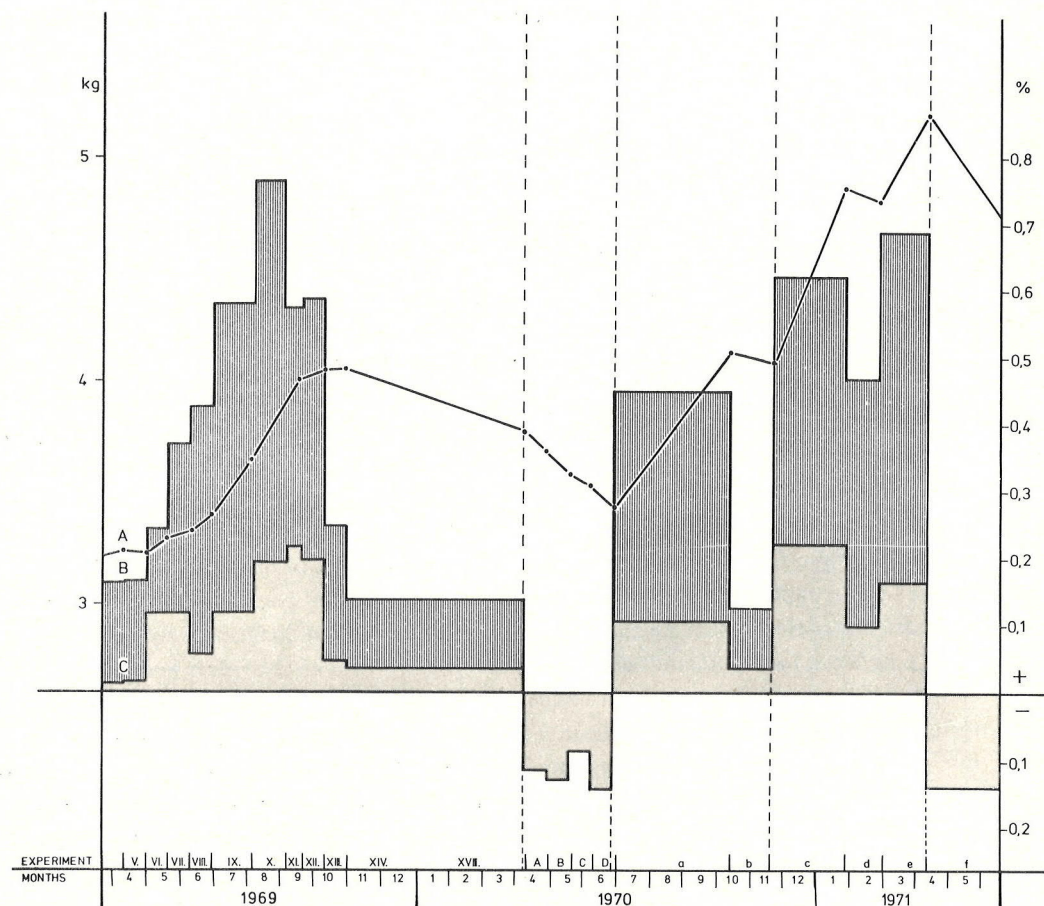


Fig. 3. Increases and decreases in weight of both experimental animals. A — mean weight of both animals; B — daily food intake of both animals as percentage of their body weight; C — weight changes of both animals expressed as percentage of their body weight.



In Fig. 3, the results of the feeding and starvation experiments are presented for the entire experimental period from 20.III.69 to 15.IV.71, as mean values for the two experimental animals. Curve A shows the mean weight of the animals in the same units as in Fig. 2 (curve C, there). Plane B represents the amount of food ingested daily by the two animals over each experiment, expressed as percentage of body weight. Plane C shows the daily increase or decrease in weight for the two animals, also calculated on the basis of their total weight.

Figures 4 and 5 give again the curves for weight (A), the values for daily food intake (Plane B), and the increase or decrease in weight (Plane C), this time calculated on the basis of the respective body weight at the beginning of each experiment. The data are given for each animal separately (for animal A in Fig. 4 and for animal B in Fig. 5), and only for the second half of the experiments, when the animals were kept separately. The two graphs more clearly illustrate the attainable levels of food intake and increases and decreases in weight than does Fig. 3. Thus the food ingestion of animal A following the long period of starvation (243 days), calculated for a period of 103 days, amounted to a daily intake of 1.113 % of the specific weight, and the daily increase in weight was 0.601 %. This gives a figure of 54 % for the fraction of the ingested food which was assimilated into the body. During "normal", i.e., rather good, growth, this value fell between 25 and 35 % (experiments VIII to XI, or c to e, Fig. 3), but these fractions were each calculated from a time period of only 60 days, at the most. The values for food ingestion and increase in weight by animal B were similarly high after the 227-day starvation period. In order to obtain comparable values, however, they should be calculated for periods of similar duration, in this case for a feeding phase of about 100 days. This can be done by drawing together the values from experiments c and d and relating them to the initial weight in experiment c. In Fig. 5, however, the data are given for shorter periods of time, for the durations of the individual experiments.

The feeding experiments, together with voluntary and forced periods of starvation, have produced a very clear result: caimans of medium size, about 1 m long and weighing between 3 and 6 kg, need food in quantities of approximately 0.2 to 0.25 % of their body weight each day to maintain their weight at temperatures between 27 and 30°C. If they eat less, their body weight decreases. If a caiman is starved for long periods at the same temperatures (they easily survive for 7 or 8 months), their body weight decreases daily by about 0.08 to 0.1 %. If an animal is well nourished at the beginning of such a period of starvation, its weight decreases more rapidly in the first weeks, up to 0.14 % of its weight daily. If food is offered in excess, the daily food intake can reach levels of 1 % of the body weight. Good growth, and at least under experimental conditions "normal" growth, is achieved by daily food intake amounting to 0.6–0.8 % of the body weight. The daily increase in weight under such feeding conditions is about 0.2 % of the body weight, but if still more food is ingested, this increase can be as great as 0.6 %. The amount of food ingested and the resultant increase in weight do not vary appreciably, whether the animals are fed only on fish or only on mammalian flesh. It should be made clear that the values for daily amounts of food were derived from the food given in each experiment, at a rate of twice a week most of the time, but in weekly series of up to five feedings in the second half of the experimental series,

divided by the corresponding elapsed time. If food was offered frequently, then only smaller portions were ingested, but if it was offered less frequently, the amounts taken in a single feeding could be larger.

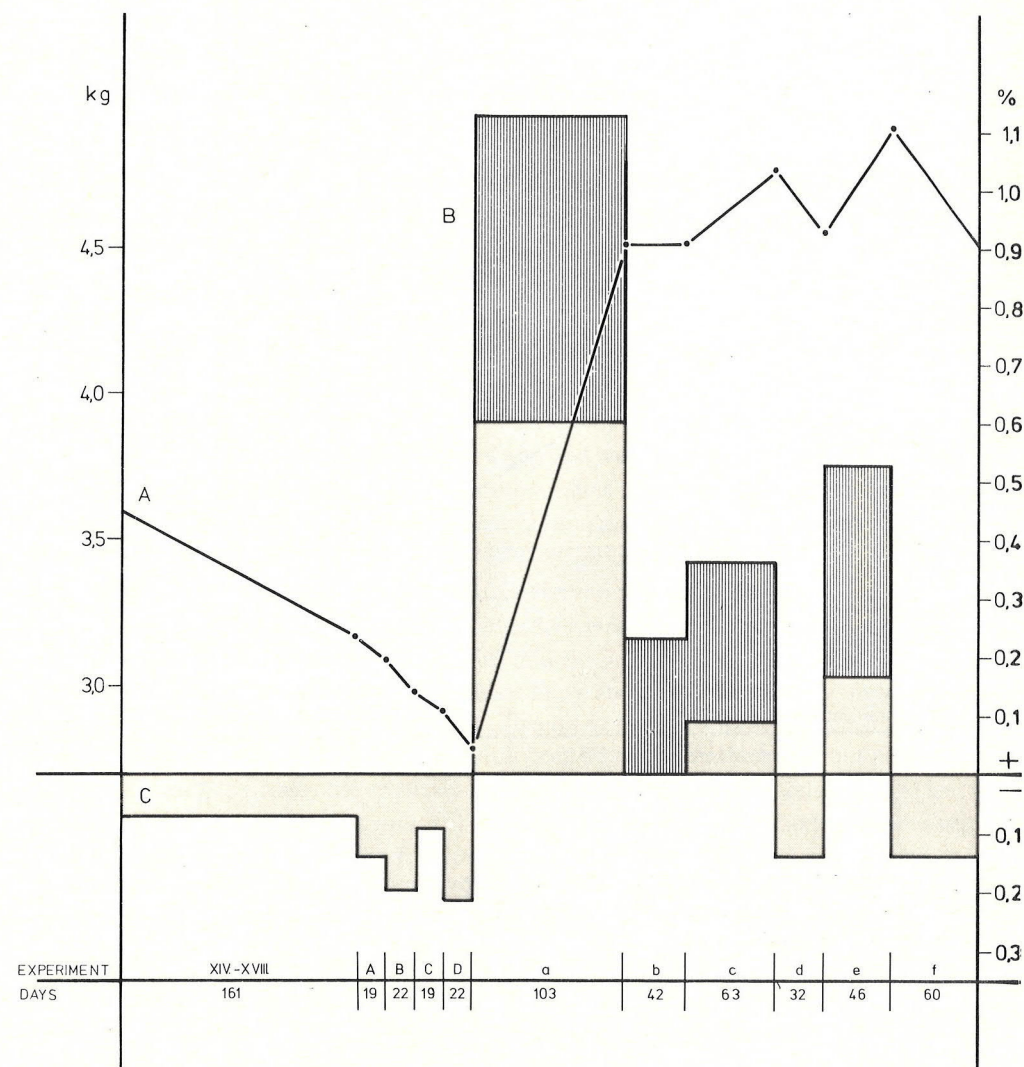


Fig. 4. Increases and decreases in the weight of experimental animal A. A— weight of the animal; B— daily food intake as percentage of its body weight; C— changes in weight as percentage of its body weight.



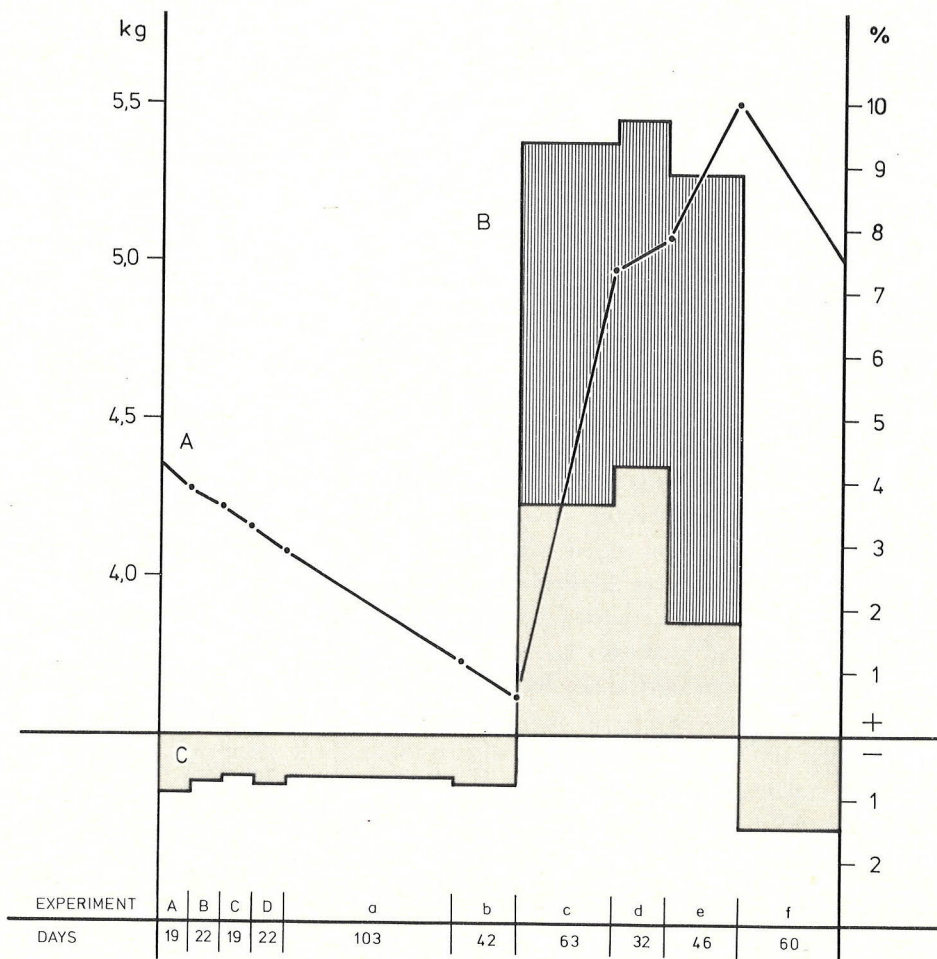


Fig. 5. Increases and decreases in the weight of experimental animal B. A — weight of the animal; B — daily food intake as percentage of its body weight; C changes in weight as percentage of its body weight.

#### Uptake and Elimination of Nutrients

The amounts of the nutrients dealt with in this study, N, P, Ca, Mg, Na and K, and provided daily per experiment with the food, were derived from total analyses of three of the food fish of various sizes (see Table 1). These values are given for experiments IV—XVIII in figures 8, 9 and 10.

N	P	Ca	Mg	Na	K	total
3,1	0,774	1,026	0,079	0,087	0,321	5,387

Table 1: Nutrient content of *Rutilus rutilus* (L.) in percentage of total fresh weight, including the viscera and their contents.

The amounts of N, P, Ca, Mg, Na and K released by the animals into the water in the experimental tanks was measured over a period of 386 days in 24 experimental periods (experiments IV—XVIII and A—C). The amounts of released nutrients, in units of milligrams per day and experiment, are given in Fig. 6; curve A gives the total weight of the two caimans and curve B the daily intake of fish per experiment.

As is evident from the experiences with food intake and weight discussed above (see Fig. 3), the animals fed well only during experiments IX—XII; that is, they ingested food at a calculated daily rate of 0.57 to 0.76 % of their body weight. During experiments IV, V, and XIV—XVIII, the daily weight of food ingested was less than 0.2 % (0.14—0.17 %) of body weight, and was therefore less than the amount required by the caimans to increase their weight. The animals, then, must apparently have mobilized food reserves in the body during these experimental periods to maintain their metabolism. This experimental series was completed with a starvation phase lasting 82 days (experiments A—C).

As was to be expected, the release of nutrients increased with increasing amounts of food. It appeared noteworthy to us, however, that the amount of nutrients released during periods of insufficient food intake (experiment IV, V and XIV—XVIII) lay in ranges corresponding to those for a period of starvation. This result appeared to be of special importance in view of the ecological function which has been ascribed to caimans within their ecosystems. Figure 7 illustrates the relatively high nutrient release at lower rates of food ingestion. Curve A represents (in percentage of food weight) the amounts of nutrients released. The contrasting curve B shows the food intake in percentage of body weight. As soon as the ingested food drops below 0.2 % of the body weight, the animals release more than 5.4 % by weight (see Table 1) of the daily ingested food as nutrients, more than were taken in during the experiment. The total released amount of the elements measured was between 0.06 and 0.1 % of the body weight during negative nutritional balance. On the other hand, values up to three times as high occurred when nutrition was good (curve B, Fig. 8).

The total amounts of nutrients taken in and released daily per experiment are given for comparison in Fig. 8. The resulting differences (clear planes) show the assimilated proportions of the total amounts of N, P, Ca, Mg, Na and K, or, during starvation phases, the amounts of the totals mobilized from body substances.



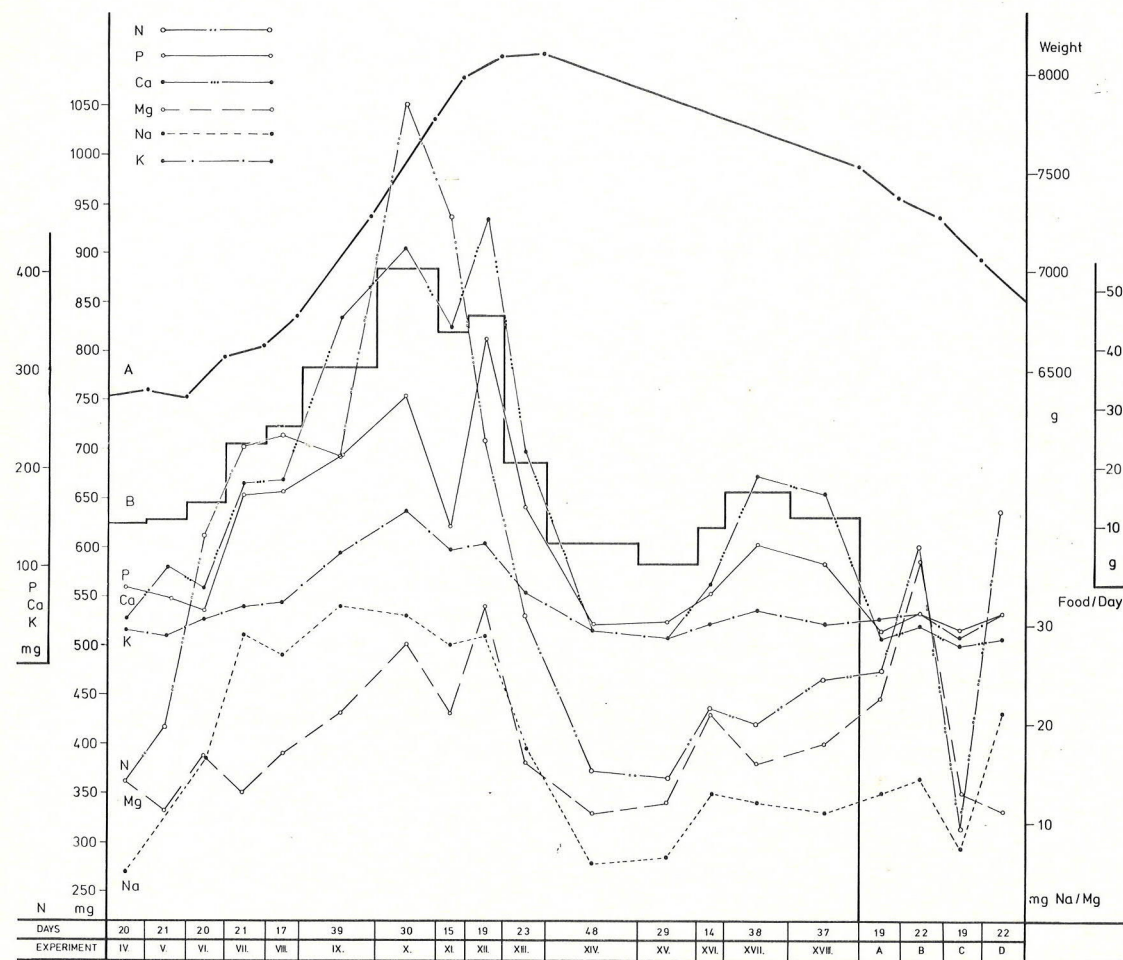


Fig. 6. The amounts of N, P, Ca, Mg, Na and K released daily over each experiment by both animals during experiments IV – XVIII. A – total weight of both animals; B – amount of food taken daily over each experiment by both animals.

The dimensions of the daily (per experiment) uptake and release of the individual elements are brought together for comparison in figures 9 and 10. It is clearly evident that during insufficient food intake and starvation, P and Ca were more effectively retained than the other elements. The release of Mg during starvation phases was relatively high. It is not necessary, however, to go into a deeper discussion of the relationships revealed here between nutrient uptake and release under varying nutritional conditions, because for our purposes only the ultimate nutrient balance is important, and not the workings of metabolism itself.

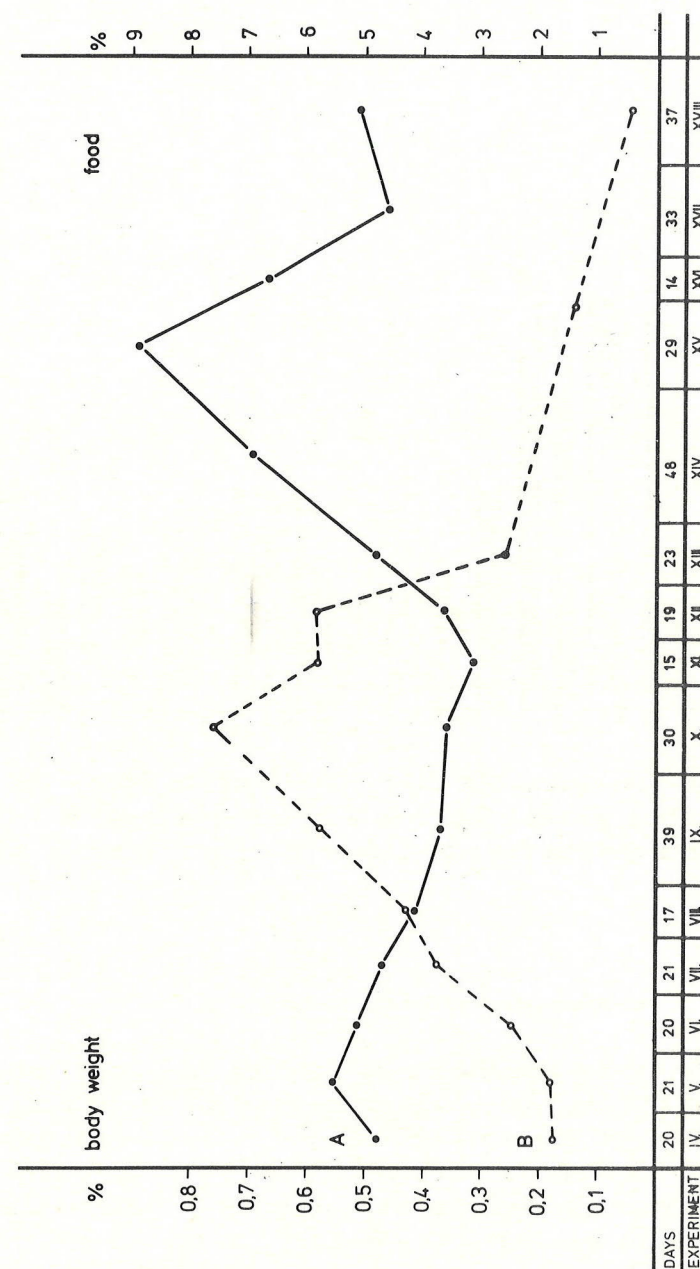


Fig. 7. Daily food intake and nutrients released by both animals during experiments IV – XVIII. A - nutrients released as percentage of the total food eaten by both. B - food intake as percentage of the total body weight of both.



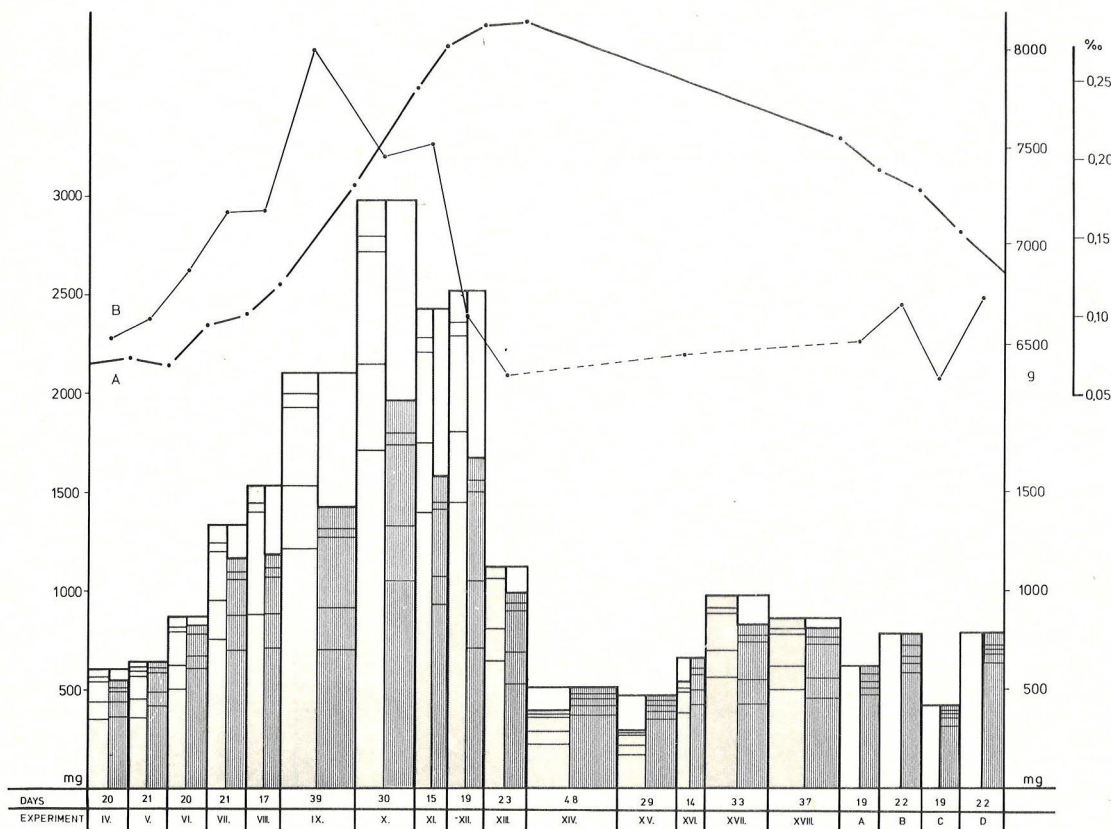


Fig. 8. Total amount of the nutrients N, P, Ca, Mg, Na and K taken in daily over each experiment with the food, and released. A— mean weight of the two animals; B— total amount of nutrients released daily over each experiment as percentage of the total body weight.

#### Conclusions from the Experiments

It may be induced from the experiments that medium-sized specimens of *Caiman crocodilus* (length about 100 to 115 cm, weight 3–6 kg) can ingest food at a daily rate of 0.6–0.8 (1.1) % of their body weight. Data in the literature support the conclusion that this feeding capacity approaches that of other, and also larger, crocodiles. COTT (1963), for example, reports that two African crocodiles about 2.3 m long and weighing about 45 kg ate 10.120 and 13.120 kg of food respectively in the form of fishes, rats and meat over a period of 36 days in captivity. These values correspond to 280 and 360 g per day, or 0.62 and 0.8 % of the body weights, respectively, and thus agree remarkably well with the values we

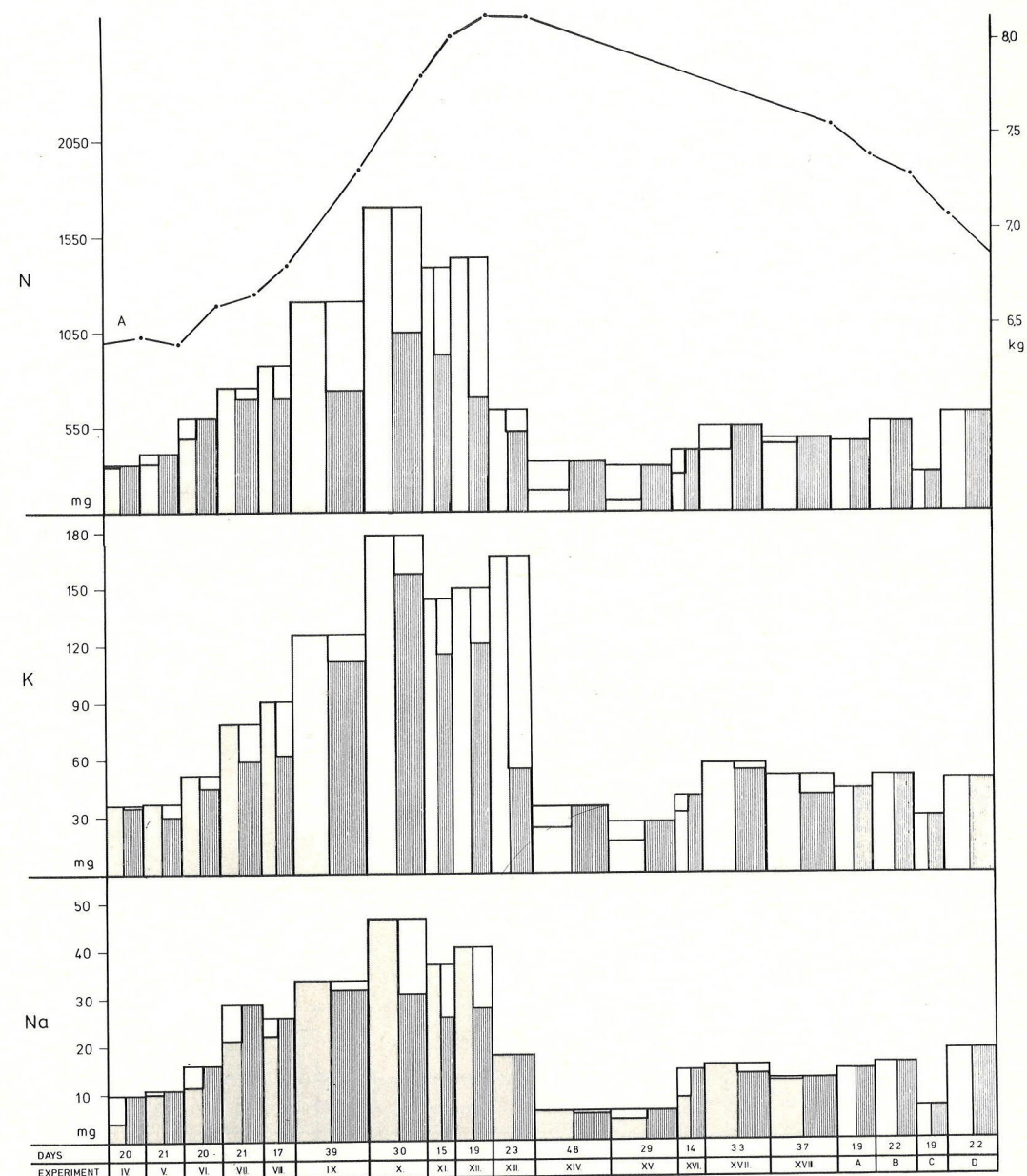


Fig. 9. The amounts of the nutrients N, K and Na taken in with the food and released daily over each experiment. A— total weight of the experimental animals during experiments IV-XVIII.



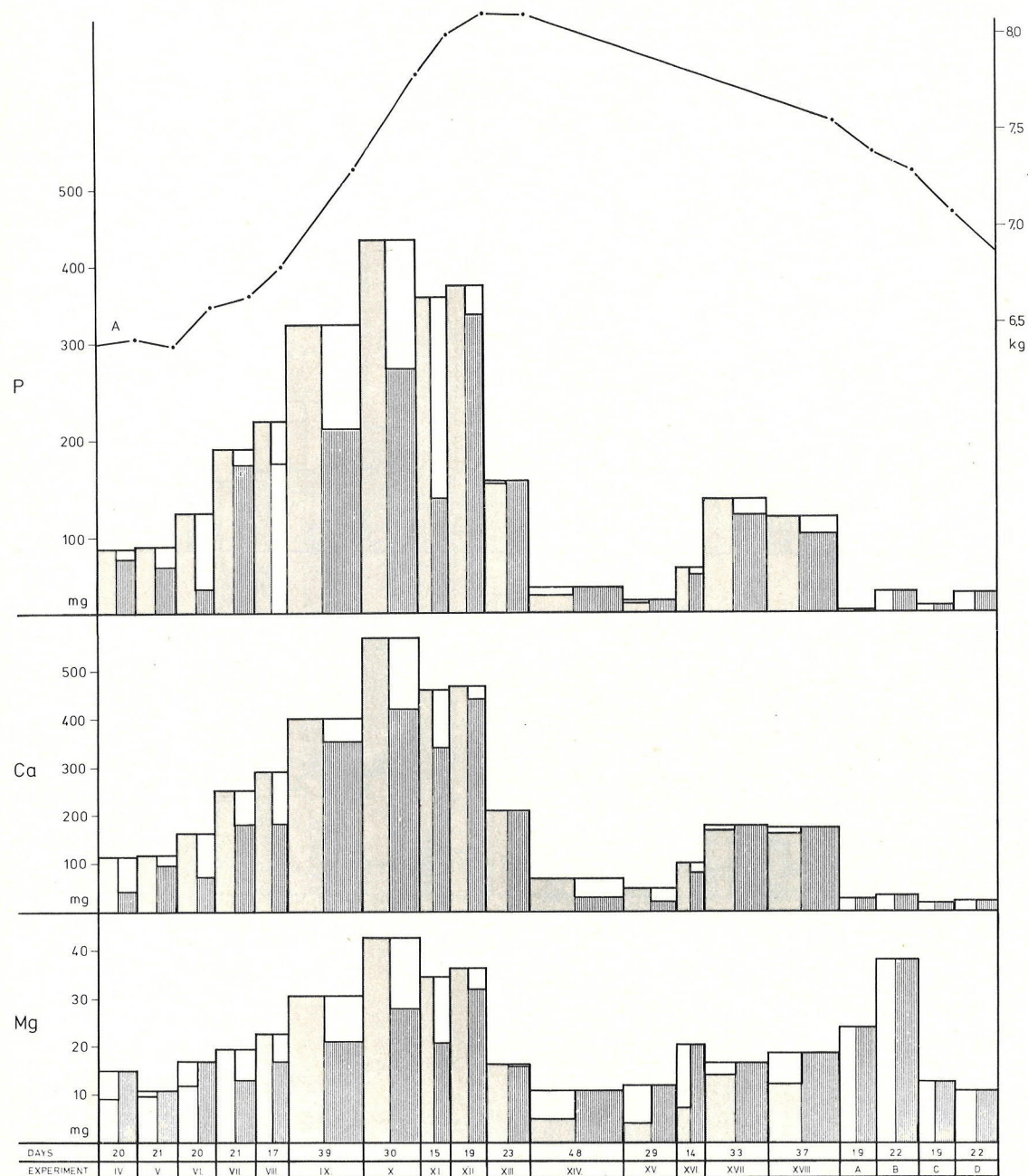


Fig.10. The amounts of nutrients P, Ca and Mg taken in with the food and released daily over each experiment. A— total weight of the experimental animals during experiments IV— XVIII.

have found for smaller Amazonian representatives of this taxon. The values given by COULSEN & HERNANDEZ (1964) refer to very young alligators, in which the feeding capacity in relation to body weight, as for young animals in general, was very much greater than for older individuals. An alligator weighing 1 kg is said in that paper to be able to eat up to 20 % of its weight in one week, which would be a daily rate of about 2.8 % of its specific weight.

Unfortunately, we know of no other observations from which we could conclude that the above agreement between values is not accidental. Since African crocodiles and North American alligators tend to grow as well in captivity as in nature (COTT 1963, McILHENNY 1934), we may be relatively sure that the agreement is due to more than pure chance.

It should be mentioned here that our experimental animals were 104 and 116 cm long on 15-VI-71, at an age of four years. This length is about the same as that of North American alligators and African crocodiles three years old. When one considers that our animals had received nothing at all to eat for a full year of their lives, and that their living conditions were in some respects very unfavorable for them, then their size corresponds well to normal development for the three years in which they fed.

For further calculations, let us take as an estimate of maximum daily food intake 0.6–0.8 % of the body weight. Then the sum of the elements N, P, Ca, Mg, Na and K released daily is 0.2 - 0.27 % and during starvation periods 0.08 - 0.1 % of the body weight. In Table 2, the percentages of the individual nutrients in the total of all nutrients are given which were released by the animals under various nutritional conditions in several experiments. For comparison, the percentage composition of these elements as measured in *Rutilus rutilus* (L.) are presented (Table 2).

With these values we are now in a position to predict, with all attainable and necessary precision, the order of magnitude of nutrients released by the caimans and made available for the ecosystem to which they belong.

In such calculations we make two assumptions: that the chemical composition of the food ingested by the caimans in Amazonia does not differ appreciably from the food we have analyzed, and, that our experimental results may be applied to animals in the freedom of Amazonian waters with validity. We have already shown above that the values measured for ingestion very probably lie in the correct range for "crocodiles" which are not very young. The few species of crocodiles which still exist on the earth today may be assigned to different taxonomic groups on phylogenetic and morphological grounds, but they show a very homogeneous pattern in their biology, physiology and biochemistry. Therefore we feel justified in generalizing the values we have obtained for released nutrients, with restrictions arising from the methods and the objectives of the study, and applying them simply to "crocodiles".

Given these assumptions, we now have the foundation at hand which we need to calculate for an (hypothetical) example the potential daily release of the nutrients N, P, Ca, Mg, Na and K under various nutritional conditions, by caimans of an Amazonian mouth-lake, or by "crocodiles" of other areas.



In the following discussion, we will consider a body of water with a surface area of  $5 \text{ km}^2$ . At low water, with a mean depth of 1 m, it will contain  $5 \times 10^9 \text{ l}$  of water, and at mean high water,  $5 \times 10^{10} \text{ l}$ . If it were an elongated, funnel-shaped mouth-lake of a river (imaginable as a drowned Pleistocene valley, see SIOLI 1968), its length would be about 10 km, its maximum width 1 km, and the total shoreline 25 km long. Under natural conditions, i.e., in no way disturbed by man, we could expect such a body of water to support a caiman population of 400 kg/ha fresh biomass, and a total caiman biomass for the lake of  $20 \times 10^4 \text{ kg}$ . If this biomass were composed exclusively of specimens 2 m long and weighing 40 kg each, their number would be about 5000, and each animal would have about 5 m of shoreline. From reliable, older reports (BATES, HAGMANN), we may state that *M. niger* was by far the most abundant species of the Amazon and its bordering waters. In the lower Amazon, there was reportedly about one *C. crocodilus* for every 20 *M. niger* in the caiman populations. *M. niger*, the jacaré-açu, often reaches lengths of 4 m; at a length of 3 m, it weighs about 100–150 kg, but at 4 m it weighs 200–400 kg. Therefore, even if we place a large number of fully grown *M. niger* in our hypothetical lake, there would still be plenty of room for younger animals.

	N	P	Ca	Mg	Na	K
a	57,5	14,4	19,0	0,15	0,16	5,9
b	51,6	14,5	23,1	0,15	0,16	7,6
c	72,3	9,7	7,7	2,4	1,4	6,5
d	77,1	6,7	4,2	3,1	2,2	6,6

Table 2: Percentages of the nutrients:

- a in the food (*Rutilus rutilus*); B, C, and D in the total nutrients released under various nutritional conditions;
- b with good nutrition (daily ingestion of 0.57 - 0.76 % of the body weight, experiments X-XII;
- c with insufficient nutrition (daily ingestion of 0.14 % of the body weight, experiments XIV-XVIII;
- d starvation phase (experiments A-C).

If we continue to consider the total biomass of caimans to be  $20 \times 10^4 \text{ kg}$ , then during the starvation phase which these animals must undergo in their natural habitat for several months of high water levels, a daily total of 20 kg of N, P, Ca, Mg, Na and K will be released into the lake. The percentages of this total due to the individual elements may be derived from Table 2, row d. The amount released would be 0.1 % of the fresh weight (see Fig. 3). With good nutrition, according to our results, the released nutrients can be double or triple the amounts released during starvation, and would therefore be about 40 to 60 kg per day. The percentage composition in individual elements would be shifted considerably toward increased amounts of P and Ca (see Table 2, row B).

The amounts of the nutrients dealt with here which would be released into a liter of lake water in 10 days under these conditions can be seen in Table 3.

	N	P	Ca	Mg	Na	K	total
I	a	3,08	0,268	0,168	0,124	0,088	0,264
	b	30,8	2,68	1,68	1,24	0,88	2,64
II	a	6,19	1,74	2,77	0,018	0,019	0,912
	b	61,9	17,4	27,7	0,18	0,19	9,12

Table 3: Quantities of nutrients in  $\gamma/\text{l}$  which would be released by a caiman population with a fresh weight of  $20 \times 10^4 \text{ kg}$  over 10 days in a lake  $5 \text{ km}^2$  in surface area; I- during the starvation period; II- with good nutrition; a - at high water (mean depth 10 m); b - at low water (mean depth 1 m).

These quantities may appear small, but they are quite sufficient to produce a decisive stimulation of primary production in the extremely electrolyte-poor waters under consideration here. The chemistry of Central Amazonian waters in the "terra firme" zone is well known (FITTKAU 1971). The amounts of the elements considered here, based on about 40 analyses of water from streams and rivers of this region, are given in Table 4.

A comparison of the quantities of nutrients given in Tables 3 and 4 shows that it is particularly those elements of special biological importance, such as Ca and P, which are very low or appear to be absent from the natural waters (Ca is present only in traces, not measurable by normal methods), and which are released in relatively large amounts by the caimans. The P which the animals provide should be of particularly great significance for the



N	P	Ca	Mg	Na	K
280	7	0	<20	1100	1050

Table 4: Quantities of nutrients in  $\gamma/l$  in Central Amazonian streams and rivers (means calculated from about 40 water samples from 30 different bodies of water).

ecosystem, because there is evidence that a large fraction of the P normally present in the water occurs in forms which can only barely be assimilated by organisms. We would not expect this to be the case for P released by crocodiles. Na and K, which constitute the smallest fractions of the nutrients released by caimans, exceed limiting concentrations in Central Amazonian waters. Even the smallest quantities of N and Mg, however, should be important in the nutrient cycles.

The effect of the nutrients provided by the caimans on the biocenosis must be especially great in the littoral zone of a lake, for it is there, in the shallow shore areas preferred by these animals, that they are concentrated. We know that a mouth-lake is a flow-through system. But, because of hydrographic phenomena, the water is retained through half the year, as was described earlier in this paper. The resulting stagnation of the water should help to cause accumulation of the released materials in regions farther from shore, as well. Moreover, a slight thermal stratification aids in isolation and retention of the upper water layers with temperatures of about 30 to 31°C, while incoming river water at 25 to 28°C flows through the lake and out along the bottom.

In order to obtain a clearer understanding of the potential functioning of the mouth-lake ecosystem, we have drawn analogies to the Central Amazonian rain forest. From it, we know that most of the nutrients which occur in limiting quantities in this system must be provided by allochthonous sources, essentially by the rain.

The same rain would also fall on "our lake", which is of course completely surrounded by the forest, and bring with it the same nutrients. Table 5 shows that the amounts of these nutrients are considerable, if we take as an estimate of rainfall the reported values (ANON. 1972) for the vicinity of Manaus for one year (which had a relatively high rainfall of 2400 mm).

The total amounts of the nutrients considered here (except Na) which are added by rainfall in that year was 16.875 kg/ha; corresponding to a daily input of 46 g/ha. In relation to the volume of our hypothetical lake, at high water 0.46  $\gamma/l$ -day, and at low water 4.6  $\gamma/l$ -day, would have been added. These amounts are about the same as those released daily by starving crocodiles. Yet the quantities of the individual elements in the rain are in different proportions from those in the lake water or in the materials released by the crocodiles, as can be seen by comparing Tables 3, 4 and 5. In a biologically very fortunate manner, then, it is precisely those nutrients which normally occur in limiting quantities in the lake

water that are supplemented most effectively by these largely allochthonous sources (see Table 6).

	N	P	Ca	Mg	total
I	10,0	0,275	3,6	3,0	kg
II	59,2	1,62	21,33	17,78	%
III	a	2,72	0,074	0,981	$\gamma$
	b	27,2	0,74	9,81	$\gamma$

Table 5: The nutrients contained in the rain falling in the vicinity of Manaus for one year (ANON. 1972): I- the amount received by one hectare in the year; II- the percentages of N, P, Ca, and Mg in the total amounts of these elements during this period; III- the amounts of nutrients added to the water in  $\gamma/l$  over 10 days; a - at high water, b - at low water, in a lake of 5 km<sup>2</sup> surface area (compare Table 3).

	N	P	Ca	Mg	Na	K
I	280	7	0	20	1100	1050
II	a	16,94	1,47	0,92	0,68	1,45
	b	34,04	9,57	1,52	0,099	5,01
III	14,86	0,41	5,39	4,50	-	-

Table 6: Nutrients and nutrient additions for a Central Amazonian mouth-lake, in  $\gamma/l$ . I- Nutrient content of the water flowing into the lake (compare Table 4); II and III- Additions of nutrients calculated on the basis of 10 days and medium high water (at a depth of 5m; compare Table 3); II- additions released by crocodiles; a- during starvation, b- during good nutrition; III- addition by rain (compare Table 5).



The quantities of nutrients which are regularly introduced by caimans into their ecosystem, and which we may assume with good cause to be predominantly of allochthonous origin, are in our view sufficient in themselves to produce a considerable increase in the primary production of electrolyte-poor Central Amazonian waters. In this way, they also enlarge the basis of their autochthonous food chain. We know, however, that caimans constitute only a fraction of the biomass which acts as a biological filter for the allochthonous sources of nutrients. We can produce no data, as has already been emphasized above, which would enable us to estimate the population density or biomass of organisms in the class, such as turtles, snakes, marsupial rats, otters and dolphins. All of these contribute to the retention or improvement of the nutrient supply. As a whole, the contribution of these groups of animals is probably no less than that of the caimans.

We should not consider and evaluate the quantities of nutrients measured or calculated here in isolation from other sources. We have already seen, through comparison with the materials added by rain, that the high levels of Ca and Mg in that source make the overall nutrient supply much more balanced and therefore more biologically beneficial. The interactions which affect the dynamics of life processes in all parts of the ecosystem must be far more complex.

None of the calculable quantities of nutrients which would be added to our hypothetical body of water would have any effect unless a functioning biological system were already present and ready to use them; and in turn, this biological system is ultimately determined by these additions of nutrients. In other words: the ecosystem functions properly only if the ecological principle which we proposed at the beginning is fulfilled; i.e., if the largest and most complexly differentiated biomass possible is present, which traps the proffered allochthonous nutrients, stores them, and retains them as long as possible in a nutrient cycle as short as possible. This ecosystem functions better, or is more stable, as its biomass becomes larger and more differentiated. The larger and richer in species is its assortment of animals, the finer is the filter for allochthonous nutrients, and the shorter are the nutrient cycles.

The special conditions arising from the hydrology of the "river-lake", the volume of water of which is exchanged at least once a year, require that the biocenosis be able to accumulate large quantities of nutrients as rapidly as they are offered, and thereafter make them continually available. The caimans are the most important fulfillers of this vital function. By now it should be very clear what the consequences would be for this biocenosis if these accumulators and transformers of allochthonous nutrients were removed from its structure.

This background enables us to understand the experiences of the inhabitants of the banks of Central Amazonian waters, and to state: the more fish-eating caimans, the more fishes there are! Therewith we can also provide a further answer to the question proposed and answered by L.J. and M. MILNE (1960) in their book, "The Balance of Nature": "Why are the crocodiles there?" In Amazonia, as in Africa or elsewhere, the crocodiles have their place and their function in the dynamic fabric of nature. May this contribution provide further material for the increasing recognition of how very easily a given ecosystem is disturbed, when man exercises his power to exterminate any one of its members.

## Summary

The example of the Central Amazonian rain forest is used to illustrate an ecological principle which determines the structure of a tropical ecosystem with a low, but balanced supply of nutrients. This principle implies that the stability of the biocenosis of such a system increases with the abundance and diversity of its species of biota, that is, the degree of differentiation and the size of its biomass. Higher abundance and diversity enable the system to take up the available allochthonous nutrients, to conserve them, and to continuously hold them in shortened nutrient cycles as efficiently as possible. In the Central Amazonian rain forest, we have an extremely large and diverse plant biomass (fresh weight), which assimilates the allochthonous nutrients supplied in the rain.

The same principle may also be recognized in the aquatic ecosystems, where the geochemical impoverishment of the Central Amazonian "terra firme" (that land which is not inundated by the annual floods of the main river system) is expressed even more severely than in the terrestrial realm. The low levels of electrolytes in the waters of such systems scarcely permit any primary production, so that here, the food chain is based directly or indirectly on allochthonous organic material. Formation of a strongly differentiated and relatively large biomass, which is mostly due to animals in macroscopic size classes, occurs only where the supply of organic material is relatively great, i.e., in the narrow upper reaches of the streams. A large number of invertebrate animals, especially insect larvae, live on bacteria and fungi. These decompose the materials such as leaves and wood, which are poor in nutrients and not directly available to the fauna. The fishes, which make up most of the biomass, act partly as direct filters for the allochthonous materials richer in nutrients, such as insects, flowers, fruit, etc. which are also contributed to the aquatic systems by the forest. As the supply of allochthonous organic material decreases relative to surface area and volume along the courses of the streams, the aquatic biocenosis becomes qualitatively and quantitatively poorer.

A new ecological situation arises in the lower reaches, which are annually backed up to form lakes. The main difference is the immigration of brooding fishes from the bordering waters of the main river system, which have high levels of nutrients and primary production. This introduces allochthonous nutrients and permits the existence of a much larger biomass. The "filters" for this periodical supply of nutrients are primarily the caimans, in addition to large piscivorous fishes, turtles, otters and dolphins. In "river-mouth lakes" which have not been disturbed by man, these predators must constitute a large proportion of the biomass.

In the Central Amazonian "river lakes", local settlers believe that the fish crops have declined following extermination of the caimans. The ecological interactions which must have existed between caimans and fishes were presented in a previous study. The present work is an attempt to determine whether the amounts of nutrients transferred by the caimans from their largely allochthonous prey, during periods of rapid growth or in longer periods of starvation, are sufficient to influence the ecosystem. The experiments showed that medium-sized caimans daily eat an amount equal to about 0.6 to 0.8 % of their body weight.



The total amounts of N, P, Ca, Mg, Na and K released daily under such feeding conditions are about 0.20 to 0.27 ‰ of their weight; when the animals are starving, this fraction is reduced to 0.08 to 0.10 ‰ of the body weight.

Based on the situation of an hypothetical (but realistic) lake with a surface area of 5 km<sup>2</sup> and a mean depth of 5 m at medium high water, the following amounts would be released over a 10-day period (in γ/l):

- a) with good nourishment: N—34, P—9.6, Ca—1.5, Mg—0.1, Na—0.1, K—5.0;
- b) during starvation: N—17, P—1.5, Ca—0.9, Mg—0.7, Na—0.5, K—1.5.

Over the same period the lake would receive in the rain, among other materials, (γ/l): N—14.9, P—0.4, Ca—5.4, Mg—4.5. The groups of nutrients added by caimans and rain complement each other in the biologically important elements, those which are present in limiting amounts in river water. (River water concentrations in γ/l: N—280; P—7, Ca—0, Mg—less than 20).

These values show that caimans daily add nutrients (mostly of allochthonous origin) in quantities that are sufficient to enable an elevation of primary production and thereby an enlargement of the autochthonous food chain based on it. With their ability to undergo long periods of starvation, during which accumulated nutrients are continuously released, the animals are especially well adapted to the ecologically extreme environment of the river-lake.

### Zusammenfassung

Am Beispiel des zentralamazonischen Regenwaldes wird ein ökologisches Prinzip aufgezeigt, das die Struktur eines tropischen Ökosystems bei einem zwar ausgeglichenen, aber sehr geringen Nährstoffangebot bestimmt. Dieses Prinzip besagt, daß die Biozönose solch eines Systems umso stabiler ist, je arten- und individuenreicher sie ist, d.h. je differenzierter und größer seine Biomasse ist; es bewirkt, daß die angebotenen allochthonen Nährstoffe jederzeit aufgenommen, gespeichert, und in einem kurzgeschlossenen Kreislauf gehalten werden können. Im zentralamazonischen Regenwald haben wir eine äußerst artenreiche, große pflanzliche Frischmasse, die die mit dem Regen zugeführten allochthonen Nährstoffe aufnimmt.

Das gleiche ökologische Prinzip ist auch in den limnischen Ökosystemen zu erkennen, wo sich noch gravierender als im terrestrischen Bereich die geochemische Verarmung der zentralamazonischen "terra firme" (das nicht vom Hauptstromsystem jährlich überflutete Land) auswirkt. Die Elektrolytarmut läßt in den dortigen Gewässern eine Primärproduktion kaum zu, so daß hier die Nahrungskette sich direkt oder indirekt auf allochthonem organischen Material aufbaut. Nur dort, wo das Angebot an organischem Material groß ist, d.h. im schmalen Gewässeroblauf, kommt es zur Ausbildung einer stark differenzierten und relativ großen Biomasse, die im makroskopischen Bereich in erster Linie von Tieren gestellt wird. Eine große Zahl wirbelloser Tiere, insbesondere Insektenlarven, leben von

Bakterien und Pilzen, die die Nährstoffarmen, nicht direkt von der Fauna nutzbaren organischen Substanzen, wie Blätter und Holz, abbauen. Die Fische, die den Hauptanteil der Biomasse stellen, wirken z.T. direkt als Filter für die nährstoffreichere allochthone Nahrung, die in Form von Insekten, Blüten, Früchten etc. dem Gewässer ebenfalls vom Wald zugeführt werden. Nimmt das Angebot an allochthonem organischen Material beim weiteren Verlauf des Gewässers ab (bezogen auf die Wasserfläche und -menge), dann verarmt qualitativ und quantitativ die Gewässerbiozönose.

Eine neue ökologische Situation finden wir in dem jährlich seenartig aufgestauten Unterlauf, dem vor allem in Form laichender Fische, die aus den angrenzenden nährstoff- und produktionsreichen Gewässern des Hauptstromsystems kommen, allochthone Nährstoffe zugeführt werden, die die Existenz einer Biozönose mit einer großen Biomasse ermöglichen. Als Filter für dieses periodische Nährstoffangebot wirken neben den großen Raubfischen, Schildkröten, Ottern und Delphinen vor allem Kaimane, die vor ihrer Dezimierung einen großen Teil der Biomasse in den vom Menschen nicht gestörten "Flußmündungsseen" ausgemacht haben dürften.

In den zentralamazonischen "Flußseen" ist, nach Meinung der Anwohner, seit der Ausrottung der Kaimane der Fischbestand zurückgegangen. Die ökologischen Zusammenhänge, die zwischen Kaimanen und Fischen bestanden haben dürften, werden in einer vorhergegangenen Studie dargestellt. Jetzt soll geprüft werden, ob die Nährstoffmengen, welche die Kaimane mit ihrem meist allochthonen Futter aufnehmen und bei gutem Wachstum oder während längerer Hungerphasen wieder ausscheiden, ausreichen können, um das Ökosystem zu beeinflussen. Die Versuche zeigen, daß mittelgroße Kaimane täglich Nahrung in Mengen von etwa 0,6 — 0,8 Prozent ihres Körpergewichtes aufnehmen. Die täglich abgegebenen Gesamtmengen an N, P, Ca, Mg, Na und K belaufen sich dann auf 0,20 — 0,27 ‰ ihres Gewichtes; hungern die Tiere, reduziert sich diese Menge auf 0,08 — 0,1 ‰ des Körpergewichtes.

Geht man von einem gedachten See mit einer Fläche von 5 km<sup>2</sup> und einer mittleren Tiefe von 5 m aus (mittleres Hochwasser) und einer Kaiman-Frischmasse von 40 g per m<sup>2</sup>, so werden pro Liter innerhalb 10 Tagen folgende Mengen (in γ) ausgeschieden:

- a) bei guter Ernährung N 34, P 9,6, Ca 1,5, Mg 0,1, Na 0,1, K 5,0;
- b) beim Hungern N 17, P 1,5, Ca 0,9, Mg 0,7, Na 0,5, K 1,5.

In der gleichen Zeit erhält der See pro Liter mit dem Regen u.a. (γ/l): N 14,9, P 0,4, Ca 5,4, Mg 4,5. Die Nährstoffzufuhren durch Kaimane und Regen ergänzen sich in den biologisch wichtigen und im Flußwasser im Minimum (in γ N 280, P 7, Ca 0, Mg <20) vorhandenen Elementen.



Die ermittelten Werte zeigen, daß Kaimane dem Ökosystem "Flußmündungssee" täglich Nährstoffe (meist allochthoner Herkunft) in Quantitäten zuführen, die zur Steigerung der Primärproduktion ausreichen und somit zur Vergrößerung der auf ihr aufbauenden autochthonen Nahrungskette beitragen können. Mit ihrer Fähigkeit, lange zu hungern, wobei kontinuierlich akkumulierte Nährstoffe abgegeben werden, sind die Tiere besonders gut dem ökologisch extremen Lebensraum "Flußmündungssee" angepaßt.

#### References

- ANON. (1972): Regenwasseranalysen aus Zentralamazonien, ausgeführt in Manaus, Amazonas, Brasilien, von Dr. Harald Ungemach. — Amazoniana 3, 186 - 198
- BATES, H. W. (1866): Der Naturforscher am Amazonasstrom. — Leipzig.
- CARVALHO, A. LEITÃO de (1955): Os jacarés do Brasil. — Arquivos Mus. Nac. 42: 127-247
- CORBET, Ph. S. (1959): Notes on the insect food of the Nile crocodile in Uganda. — Proc. Roy. ent. Soc. Lond. (A) 34 : 17 - 22
- CORBET, Ph. S. (1960): The food of a sample of crocodiles (*Crocodilus niloticus*) from Lake Victoria. — Proc. Zool. Soc. Lond. 133 : 561-572
- COTT, H. B. (1963): Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. — Trans. Zool. Soc. London 29 : 211-337
- COULSON, R. A. and Th. HERNANDEZ (1964): Biochemistry of the alligator. A study of metabolism in slow motion. — Baton Rouge.
- FITTKAU, E. J. (1970): Role of Caimans in the nutrient regime of mouth-lakes of Amazon affluents. — Biotropica 2 (2) : 138-142
- FITTKAU, E. J. (1971): Neues Material zur geochemischen Gliederung des Amazonasgebietes. — Zweites Symposium des Max-Planck-Institutes für Limnologie Plön und des Geographischen Institutes der Universität des Saarlandes über Biogeographische und Landschaftsökologische Probleme Südamerikas.
- FITTKAU, E. J., W. JUNK, H. KLINGE und H. SIOLI (1961): Substrat und Vegetation im Amazonasgebiet. 13. Int. Symposium über Vegetation und Substrat, Rinteln (im Druck).
- FITTKAU, E.J. and H. KLINGE (1973): On biomass and trophic structure of the Centralamazonian rain forest ecosystem. — Biotropica (im Druck)
- HAGMANN, G. (1902): Die Eier von *Caiman niger*. — Zool. Jahrbuch (Syst.) 16 : 405-410
- HAGMANN, G. (1909-1910): Die Reptilien der Insel Mexiana, Amazonasstrom. — Zool. Jahrbuch (Syst.) 28 : 473-504.
- KLINGE, H. and W. A. RODRIGUES (1968): Litter production in an area of Amazonian terra firme forest. I, II. Amazoniana, 1 (4) : 287-302, 303-310.

- KNÖPPEL, H. —A. (1970): Food of Central Amazonian Fishes, Contribution to the nutrient-ecology of Amazonian rain-forest-streams. — Amazoniana 2 (3): 257-352
- MEDEM, F. von (1958): The crocodilian genus *Paleosuchus*. — Fieldiana, Zool. 39 : 227-247
- MEDEM, F. von (1963): Osteología craneal, distribución geográfica y ecología de *Melanosuchus niger* (Spix). Rev. Acad. Columb. Cienc. 12 : 5-19
- MEDEM, F. von (1967): El género *Paleosuchus* en Amazonia. Atas do Simpósio sobre a Biota Amazônica 3 (Limnologia): 1-7.
- Mc ILHENNY, E.A. (1934): Notes on incubation and growth of alligators. — Copeia 1934 : 80-88
- SATTLER, W. (1963): Über den Körperbau, die Ökologie und Ethologie der Larve und Puppe von *Macronema Pict.* (Hydropsychidae), ein als Larve sich von "Micro-Drift" ernährendes Trichopter aus dem Amazonasgebiet. — Arch. Hydrobiol. 59 : 26 - 60
- SATTLER, W. (1967): Über die Lebensweise, insbesondere das Bauverhalten, neotropischer Eintagsfliegenlarven (Ephemeroptera, Polymitarcidae). — Beitr. neotrop. Fauna 5 (2) : 89-110.
- SIOLI, H. (1968): Zur Ökologie des Amazonas-Gebietes. — In: Biogeography and Ecology in South America. 1 : 137-170. Monogr. Biol. 18, W. JUNK. The Hague.
- WERMUTH, H. (1953): Systematik der rezenten Krokodile. — Mitteilg. Zool. Mus. Berlin 29 (2) : 376-514

Author's address:

Dr. E. J. Fittkau  
Max-Planck-Institut für Limnologie  
Abteilung Tropenökologie  
D-2320 Plön (Holst.)  
Germany